On the Method of Oviposition and the Egg of *Lyctus brunneus*, Steph.

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(Plate 12 and 2 Text-figures.)

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Contents.

Introduction.

In April 1920, the writer commenced an investigation on *Lyctus*—Powder-post—beetles attacking seasoned hardwoods, with a view to devising control measures against their ravages.

This paper is a part of one originally written dealing with all those various aspects of *L. brunneus* which had not been recorded, but owing to the cost of getting the whole published, it has been found necessary to cut it up into sections, and this constitutes the first part.

There are two species of beetles of the genus *Lyctus*, family Lyctidæ, so far recorded in the British Isles. They are *Lyctus* (*Xylotrogus*) *brunneus*, Steph., and *Lyctus linearis*, Goeze (*canaliculatus*, Fab., *oblongus*, Oliv., *striatus*, Melsh., *unipunctatus*, Herbst). Both species breed in dry or seasoned hardwoods, usually attacking the sapwood only, although *L. brunneus* was found attacking the sap- and heartwood of mahogany (*Khaya* sp.), and Noerdlinger (1862) recorded *L. linearis* as attacking sap- and heartwood of black locust (*Gleditschia triacanthos*).

In 1891 Fowler recorded *L. brunneus* as very rare, and *L. linearis* (*canaliculatus*) as common; the contrary is now the case. Hopkins (1911) considers *brunneus*—now widely distributed throughout the world—to be of S. American origin, and *linearis* of European origin.

Review of the Literature.

Amongst the mass of literature on Powder-post beetles, there has been very little published upon *L. brunneus*, and what there is deals mainly with its

ravages, but on the other *Lyctus* beetles there are some descriptions of oviposition, and in three cases an egg is described.

In 1853 Heeger figured and described an egg, a legless larva, and a pupa, which he ascribed to *L. pubescens*, Panz.

In 1855 Noerdlinger described the larva, pupa, and adult of *L. linearis* (*canaliculatus*), and in an account of the habits stated that the eggs were deposited in cracks or fissures.

In 1874 Kaltenbach refers to the habits of the larva of *linearis* (*canaliculatus*) and to that of *pubescens*, quoting Heeger as his authority in the case of the latter.

In 1876 Perris described and figured the larva of *linearis* (*canaliculatus*), and disputed the accuracy of Heeger's description of a legless larva of *pubescens*.

In 1880 Kittel described—after Noerdlinger (1855)—the larva, pupa, and adult of *linearis* (*canaliculatus*).

In 1883 Dugès described and figured the larva, pupa, and adult of *L. planicollis*, Le Conte (*L. carbonarius*, Waltl.), to prove that the legless larva described and figured by Heeger could not belong to the genus *Lyctus*.

In 1890 Rye refers to the discovery of a legless larva of "a species of *Lyctus*" (?).

In 1898 Xambeu described the life-history of *linearis* (*canaliculatus*) including a description of the egg, and stated that the eggs were deposited in cracks or fissures; this description was corroborated by Bureau (1900), and since by several writers.

In 1916 Snyder described the egg and manner of oviposition of *planicollis*, and figured the egg. This egg differs from that of *pubescens* as described and figured by Heeger, and from that of *linearis* as described by Xambeu, but it is practically identical in appearance with the egg of *brunneus* found by the writer. This similarity between the eggs of *planicollis* and *brunneus* is maintained up to the time of maturation of the larva (Pl. 12. fig. 4), but the method of the larva's hatching differs.

Oviposition in *brunneus* is similar to that of *planicollis*, and it is not as described by French in 1918, who states :—"The female (*brunneus*) deposits her eggs on the outside, underside, and ends of the timber." The eggs are deposited inside the timber.

Material used.

Most of the infested material from which *L. brunneus* was bred was obtained in London from hardwoods stored in a timber yard, where the presence of the beetle had been known for a few years.

Pieces of infested wood were collected in April 1920. The beetle was then still in the larval stage. In May of the same year, a small quantity of the infested material was placed in a refrigerator with a constant temperature

of 8° C. to retard development; this material was withdrawn in July 1920 and enabled the writer to verify the observations on oviposition and the egg at leisure.

The infested woods collected were West African mahogany (*Khaya* sp.), "Wainscot" oak (*Quercus Robur*), and "Italian" walnut (*Juglans regia*). Beetles were also bred from locust (*Robinia pseudacacia*).

Unfortunately no living specimens of *L. linearis* were obtained, although efforts were made in various directions to procure some. No beetles emerged from two pieces of oak—hitherto infested with *L. linearis*—which were sent over from Paris, nor were any living larvæ or pupæ found. Dr. C. J. Gahan informed the writer, that no record of the capture of this beetle in the British Isles had come to his notice for some years.

Mating.

The beetles are sexually mature when they emerge. Mating takes place immediately after emergence either at dusk or during the night. It was observed in daytime; and on several occasions two beetles were found occupying the same pupal chamber, but in no instance was mating observed to last very long. Individual males fertilize several females, therein differing from *L. linearis* as described by Xambeu (1898), who stated coition lasted the entire night and the male then dies. In *brunneus*, females considerably outnumber the males.

The length of the life of the females when free to mate and oviposit averaged about six weeks; the males lived two to three weeks. The food of the adults consists of particles of wood-tissue.

Oviposition.

The ovipositor is an exceedingly long and flexible organ, and when fully extruded (Pl. **12**. fig. 1) it is nearly the length of the beetle.

Oviposition begins two to three days after mating and takes place, at dusk or during the night, in the tracheæ, or vessels, or pores of the wood. Consequently those woods in which the vessels are most numerous are most liable to heavy attacks.

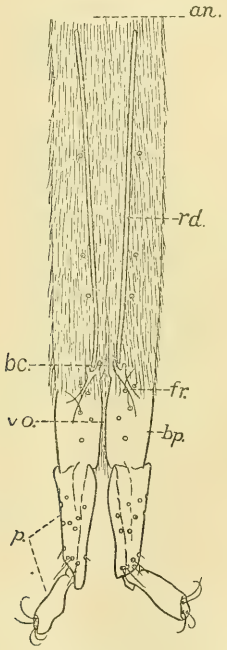
The female either projects the ovipositor directly into the vessel, or it is curved down and bent forward in the vessel underneath the body. Before actually inserting the ovipositor into a vessel, a preliminary examination of the surface is made with the ventral pygidial palps, and after selecting a vessel the ovipositor is slowly inserted, and apparently a further examination is made within the vessel by the vaginal palps (*p*, text-fig. 1) on the apex of the ovipositor; when, if the conditions are suitable, two or more eggs are deposited. The number, however, depends upon the suitability and capacity of the vessel. For, when an obstruction is encountered—in the form of broken down transverse walls, etc.—only one or two may be deposited, or the ovipositor will be withdrawn and another vessel tried.

The eggs are always laid longitudinally in the vessel and in juxtaposition, the anterior pole of one being end on to the posterior pole of the next.

A female will retain the ovipositor in the vessel for several minutes, and repeat the process in other vessels until her supply of ripe eggs is exhausted.

The egg issues from the vaginal orifice (*vo.*, text-fig. 1) between the basal pieces (*bp.*), and is guided by the vaginal palps (*p.*).

TEXT-FIG. 1.



Apex of the ovipositor, ventral. *an.*, anus; *bc.*, bursa copulatrix; *bp.*, basal piece; *fr.*, forked rod; *p.*, vaginal palp; *rd.*, chitinised rod; *vo.*, vaginal orifice. *Camera lucida.* (×128.)

From observations on a beetle when ovipositing, it was noticed that she moved forward once before withdrawing the ovipositor; apparently the movement was just far enough to allow for a space for the second egg to be deposited in

Oviposition also takes place—in the case of previously infested wood—in those vessels which have been bitten across in the pupal chamber and its extension to the exit-hole.

It was observed that, when the beetles are feeding on the surface of the wood, they always bite the tissues transversely; this habit—if the wood is longitudinally split—not infrequently cuts open a vessel and creates a point of access to it. In several instances, examination has shown that this opening in the vessel has been used for the deposition of eggs.

The eggs are deposited in the vessels at varying distances from the point of access of the ovipositor, but the anterior pole of the last egg laid is seldom less than 1 mm. from it. In one specific instance in which three eggs were found, the distance from the point of access to the posterior pole of the first egg deposited was 3·75 mm.; on two occasions five eggs in juxtaposition were found, in these cases the ovipositor had been inserted more than 5 mm.

The eggs were difficult to find and very easily broken when shaving off the wood-tissues in search of them, and when exposed, the task of removing them or "digging" them out is an exceedingly difficult one. The writer estimates that on an average 75 per cent. of the eggs were lost in trying to locate them, and probably 60 per cent. of the located eggs were damaged or destroyed in endeavouring to extract them from the vessels.

From the examination of several ovaries, it was found that in the case of fertilized females, only a small number of eggs mature at a time, eight to twelve being the usual number found collected in the calices. In the case of unfertilized females, the ripe eggs continue to pass into the calices until the latter become swollen and the death of the female ensues.

The Egg.

Pl. 12. fig. 2 is a photograph of deposited eggs *in situ*; part of the vessel and surrounding tissues have been removed.

The egg is translucent white and cylindrical; tapering towards and rounded at the posterior pole. The anterior pole is rounded, but continuing from it, as if broadly attached to it, is a long, slender tube-like process which terminates in a round protuberance.

This process varies considerably in length even in those eggs laid by one female. The process was never observed to be attached to the walls of the vessel, but when two or more eggs had been deposited in the same vessel it was usually found adhering to the egg next to it.

The chorion is creased longitudinally, giving the egg the appearance of being marked with longitudinal striæ, which concentrating at the anterior pole are more pronounced in this area. These striations and the process or strand were found to owe their origin to the action of chitinised setæ lining a pair of valves situated at the junction of the oviducts, and are the result of the pressure exerted by the valve upon the egg as it is forced through on its passage.

A ripe egg removed from the calices of a female does not show the process or striations, and would thus agree with Xambeu's (1898) description of the egg of *L. linearis*.

The recently deposited egg (Pl. 12. fig. 3) has a distinct granular appearance, due to the exceptionally large yolk granules.

The size of the deposited eggs was found to range from 1·25 mm. to 0·8 mm. in length without the process, which varied in length from 0·2 mm. to 0·35 mm., and the width of the egg ranged from 0·15 mm. to 0·175 mm. During maturation the egg slightly increases in size.

In eight specific instances, comprising 13 eggs under observation, the young larva reached maturity 15 days after the egg was laid. That is, movements of the larva were visible within the chorion at that period. The actual number of hours any of these eggs took to reach this stage is not known, as the time at which oviposition took place was not observed. But the small pieces of wood in which the beetles were allowed to oviposit were put in their cages—glass-topped tins—in the evening and collected the following morning, 12 to 16 hours later.

At the time of maturation or when the first movements of the larva are visible, it occupies approximately half the length of the egg (Pl. 12. fig. 4) and is situated in the posterior portion ; the anterior portion, from the base of the process to the head of the larva, is occupied by a mass which consists of large yolk granules and fat bodies. The writer has observed that this extraordinary mass* constitutes in *L. brunneus* the initial food of the young larva whilst still enclosed within the chorion.

In the case of *L. planicollis* it is stated that: "In hatching, the larva backs out of the egg" (Snyder, 1916). It is the reverse with *L. brunneus*. So soon as the larva is matured, it commences to eat the residual yolk-mass situated in the anterior portion of the egg by means of its mandibles, and travels forward to do so. If an egg is completely exposed in the vessel, the larva is unable to consume the entire residual yolk-mass, owing to its movements and the lack of "overhead" support—the wall of the vessel—it usually breaks the chorion and works its way out of the vessel. But if small strips of tissue, such as parts of a medullary ray, are left above part of the egg, the larva is able to maintain its position and consume its food, and at the same time the observer is enabled to follow its normal movements.

An examination of longitudinal and transverse sections of a small number of eggs in different stages of development, suggest that the phenomenon of the residual yolk-mass is due to the blastoderm enveloping only a part of the yolk. It was thought that it might be a case of polyembryony, with one or more embryos abortive, but there was no evidence found to support this.

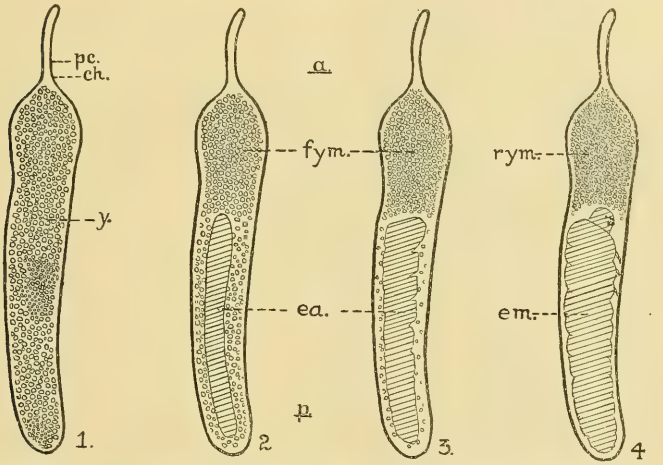
* Owing to the lack of an existing term for this "yolk-mass"—no analogous yolk-mass being known—the term residual yolk-mass has been suggested and is used in this paper to denote it.

Text-fig. 2 gives a series of diagrammatic sketches showing the maturation of the egg in four stages.

The movements of the larva are easily discernible within the intact covering of the chorion, and it is not until the larva has been feeding for some time that the chorion becomes broken by its movements at the posterior end and later injured in the process of the consumption of its initial food.

Pl. 12. fig. 4 depicts an egg in which the larva has commenced feeding on the residual yolk-mass in which its head is partially buried. (The bend in the egg was due to the movement of the larva when dropped into Carnoy II.) The photo shows that the chorion at the posterior end is broken, and that it is crumpled in the part occupied by the larva, whereas it is quite taut around the anterior part.

Text-fig. 2.



Development of the egg (diagrammatic). 1. Egg twelve hours old. 2. Several days later. 3. About ten days old. 4. Mature egg.

a., anterior pole; *ch.*, chorion; *ea.*, embryonic area; *em.*, embryo; *fym.*, formation of residual yolk-mass; *p.*, posterior pole; *pc.*, process or strand; *rym.*, residual yolk-mass; *y.*, yolk.

Locating the Eggs.

In the first instance the beetles were caged in a cavity (1½ inches in diameter) cut with a brace and bit in pieces of mahogany (4 inches by 3 inches by 1 inch thick). The cavity, which was full of cracks, fissures, and crevices, was about ½ inch deep, and it and the surface of the piece of wood were covered with a piece of glass held in position with elastic bands.

Shaving off the wood with a scalpel under binoculars in search of the

eggs, after the manner of oviposition was established, proved far from satisfactory and extremely laborious owing to the mass of wood which had to be cut away from the sides to shave down those parts to get near the vessels which had been opened transversely and accessible to the beetles. And so another and entirely successful method was adopted.

Glass-topped tins were used as cages. Into these small pieces of mahogany were put for the beetles to oviposit in. The sizes of these pieces, which were split on all faces longitudinally with the vessels, and cut transversely at the ends, ranged from 1 to 2 inches in length by one-eighth to about three-eighths of an inch in width and thickness.

The search for the eggs in these pieces was carried out as above and was mainly confined to the extremities, unless a vessel had been fractured in splitting or bitten open by a beetle.

No attempt was made to find eggs in planks or in the "field."

Note on *Lyctus linearis*, Goeze.

As no living specimens of *L. linearis* were obtained, the writer's intention, to study the early stages of this insect with a view to critically examining the descriptions of the manner of oviposition and the egg as published by Noerdlinger (1855) and Xambeu (1898), did not materialise.

Several writers since 1898 to 1920 have published corroborative accounts of Xambeu's description of the egg and manner of oviposition. But it has recently been found that in 1917 Hopkins and Snyder—after the latter's discovery of the egg and manner of oviposition of *L. planicollis*—published a paper in which they described the life-histories of *L. linearis*, *L. parallelopipedus*, Melsh., *L. cavicollis*, Lec., and *L. planicollis*, as being identical except as to the time of the emergence of the adults. The inference to be drawn is that the egg and manner of oviposition is similar in these four species and consequently similar to the egg and manner of oviposition of *L. brunneus* as described in this paper.

Therefore Xambeu's description of a strandless egg deposited in cracks, fissures, or crevices can no longer stand.

It will probably be found that this method and manner of oviposition—depositing the eggs in the tracheæ, vessels, or pores—is a generic characteristic of the wood-infesting *Lyctus* beetles.

Conclusions.

The phenomenon of the egg of *L. brunneus* is, so far as it has been possible to ascertain, unlike any case of embryological development recorded, not only in the records of Entomology, but in those of Zoology as a whole; a case in which within the egg is produced the young larva's initial food.

The closest analogy found is that of a case of polyembryony discussed by Gatenby (1919) in a review on the early development of the egg and the

formation and maturation of the larvæ of a polyembryonic *Encyrtid* (Parasitic Hymenoptera), in which he refers to the existence of abortive embryos. He states: "It is remarkable to find that in the polyembryonic Hymenoptera a large region of the egg is entirely discarded. In fact, just that region of the egg which would have formed the head, brain, etc., of the embryo is rejected."

It is the same area in the egg of *L. brunneus* which becomes the larva's initial food.

The similarity of the egg of *L. brunneus* to that of *L. planicollis*—as described and figured by Snyder (1916)—in their appearance up to the time of maturation, suggests that the embryological phenomenon of the former species must also exist in the latter.

Summary.

1. The method and manner of oviposition in *L. brunneus* is established and is found to be the same as in *L. planicollis*, which is that of depositing its eggs in the tracheæ, vessels, or pores, and under the surface of the wood.

2. The eggs incubate in 15 days. The young larva, which occupies barely half the length of the egg, does not hatch out at once, but proceeds to eat the residual yolk-mass contained in the anterior part of the egg.

Acknowledgments.

The investigation, of which this paper records part of the results, was suggested by Prof. H. Maxwell Lefroy, Imperial College of Science, to whom the writer has to express his thanks, and to the Committee of the Scientific and Industrial Research Department, for a grant to carry on the work.

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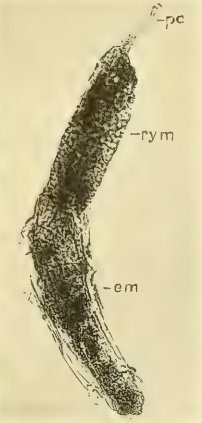

A.M.A. Phot.

Westwood Bequest

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EXPLANATION OF PLATE 12.

Fig. 1. Photomicrograph of female *L. brunneus*, with ovipositor fully extended; magnified 7 diameters.
2. Two eggs *in situ* in a piece of mahogany.
3. Photomicrograph of an egg, 12–16 hours old.
4. Photomicrograph of a mature egg.

(Fig. 1 by C. Gunns; figs. 2–4 by A. M. A.)